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Research Article

Defensive phragmosis and cathaptosis in Trichoptera larvae

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Abstract

Phragmosis, or the use of specially modified body parts and associated behaviors to block an opening as defense against predators, is a commonly observed phenomenon in certain ants and termites that block entrances of their subterranean nests with large, flat heads. It has been reported in some beetles and other insects and even in some frogs. Common features of phragmosis in caddisfly larvae include a hard and usually flat body surface, with or without stout spines, and the behavior of fitting that body surface tightly in the opening of its case. A different defensive strategy occurs in snails and case-making larvae of camptosomate leaf beetles (Chrysomelidae: Cryptocephalinae and Lamprosomatinae) that protect themselves from predators by securing the openings of their shells or cases firmly against the substrate, a behavior we call "cathaptosis." Common features of cathaptosis in caddisfly larvae include a case with its vulnerable opening oriented parallel with the substrate and accompanied by behavior that grips the substrate, fixing the case opening firmly against it when threatened. We suggest that these defensive strategies have evolved multiple times in Trichoptera, especially in case-making larvae. We demonstrate some examples and provide tentative lists of caddisflies whose larvae may have evolved these defensive strategies.

Key Words

behavior, case, cover, evolution, predator, shield

Introduction

A "chokepoint" is an important strategic passage through an otherwise impassible territory, usually substantially narrower than that territory, which greatly decreases the advantage of a superior attacker. In a military context, King Leonidas I's leadership of the Spartans to defend the narrow Pass of Thermopylae during the Persian invasion of Greece, led by Xerxes I on 21 August 480 BCE, serves as an historic example. "Phragmosis" (from φράγμα, pronounced "frágma," meaning "barrier" or "shield") is a similar evolutionary strategy that integrates a specialized morphology (shield) and a corresponding behavior to defend a narrow opening (chokepoint) by a single individual or small group of individuals, described originally for the structure and behavior of certain species of soil-nest-building, colonial ants (Wheeler 1927). When an animal lives in a protective nest, an opening for egress and ingress is a vulnerable threshold for potential attack by a predator or parasite. One way to protect this threshold from intruders is for residents to evolve both a morphologically near-impenetrable surface (usually a hard, flat, thick body part, a "shield") that fits the entryway and a behavior to use that surface for blocking the entrance when threatened. To be effective, there should be little if any structure on the shield that can be grasped by a predator, but there may be sharp spines, dense hair, or other features that can serve to help deter or repel the intruder. In insects, usually the

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head (with thoracic nota sometimes included) or the end of the abdomen evolved an especially hardened area that is typically truncate and with edges that fit the entrance of their nest and that the insects use to block the entrance of the nest. We propose to expand this concept of phragmosis to include structures and behaviors to block the entrance of a portable and protective case or shell. Does this phenomenon occur in at least some case-bearing caddisflies?

Alternatively, some encased animals defend the chokepoint opening of a portable case or shell by pressing it against impenetrable substrate. Such a case or shell has only one opening and the shape of that opening conforms to the shape of the impenetrable substrate. The encased animal may also have adaptations that help it to hold itself especially tightly against the substrate. We term this structure and behavior "cathaptosis" (from καθάπτω, pronounced kathάptō, meaning to fasten or make fast) to describe the behavior of grasping the substrate firmly and holding it tightly against the shell or case opening. Does this phenomenon also occur in at least some case-bearing caddisflies?

Phragmosis

In the family Hylidae, a tree frog *Corythomantis greeningi* Boulenger, 1896 has a phragmotic head (including the eyelids) with flat, rough, and venomous properties (Jared et al. 1999; Mendes and Barbaro 2016). The rough texture of the head also allows it to appear like bark for better concealment. The frog's neck is sufficiently mobile to permit positioning the flat head at a 90-degree angle to the burrow's opening for hours to days at a time (Fig. 1), behavior that has been documented as phragmotic (Jared et al. 1999, 2005; Paluh 2020). Other frog species, such as *Apurasphenodon brunoi* Miranda-Ribeiro, 1920, live in the leaf axils of bromeliads and show similar behavior and morphology (Andrade and Abe 1997; Pimenta 2009).

Some arachnids are phragmotic. For example, trapdoor spiders are known to create a tunnel in the ground, coating it with silk, and giving it a tightly fitting cover or "door" made of silk and debris. Some trapdoor spiders, in genera such as *Cyclocosmia* Ausserer, 1871 (Fig. 2)

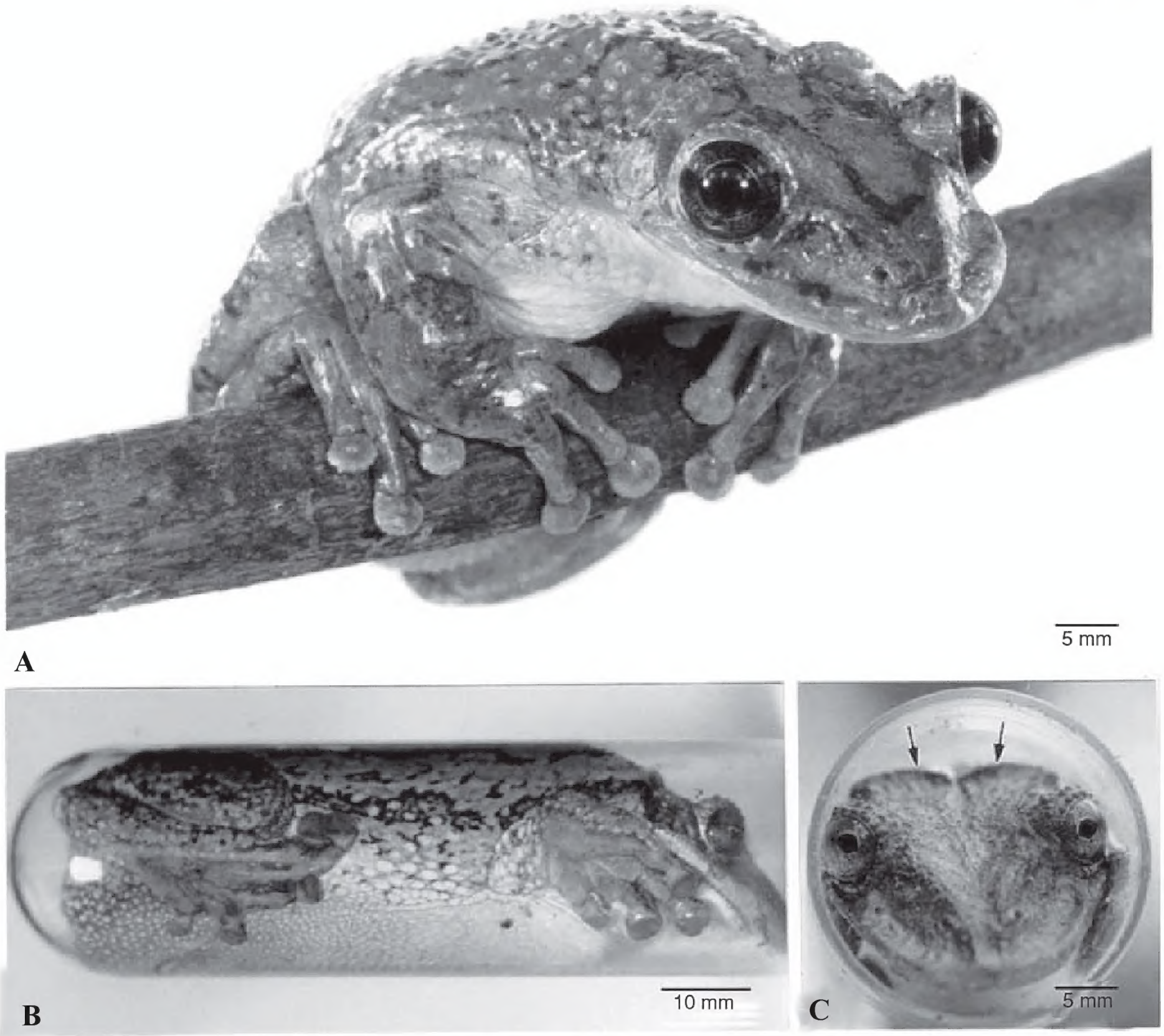

Figure 1. The casque-headed tree frog *Corythomantis greeningi* Boulenger, 1896 (Hylidae) (from Jared et al. 2005). **A.** Habitus; **B.** Female in phragmotic posture inside test tube, with head bent and head top exposed to exterior; **C.** Inside test tube, frontal view, with co-ossification area clearly delimited and arrows pointing to well-delimited posterior region of head.

and *Ummidia* Thorell, 1875 (Arachnea, Ctenizidae) each have a phragmotic abdomen (Schwendinger 2005; Xu et al. 2017). They use their truncated and often thick and tough abdomen to protect themselves in their tunnel from predators (such as birds, scorpions, and snakes) if the trap door is breached (Bond and Coyle 1995). The camouflaged and tough trapdoor and the hard abdomen serve as primary and secondary defenses, respectively (Gertsch and Platnick 1975; Zhu et al. 2006; Rix and Cooper 2017).

Among eusocial groups, soldiers or workers of some ants (Formicidae) have phragmotic heads and behaviors (Creighton 1953; Cloudsley-Thompson 1962). For example, in *Colobopsis nipponicus* Wheeler, 1928, workers employ phragmotic heads to barricade the nest threshold from intruders (Fujioka et al. 2019). In genus *Camponotus* Mayr, 1861, the relationship was described as follows: "The nest entrances are neat, circular holes into which the heads of the soldiers fit snuggly" (Wilson 1974). There is repeatedly a close relationship between the size and shape of the phragmotic portion of the insect and the size and shape of the threshold or chokepoint.

Other ants have evolved unique approaches for employing phragmotic defense. For example, a rare cooperative phragmotic defense has been reported in the genus *Cephalotes* Latreille, 1802 (Formicidae). Several workers and/or soldiers, depending on the species, collectively use their phragmotic heads to block large or irregular nest openings by having multiple ants assemble and obstruct the opening with a multi-organismal wall (Powell 2008). Interior pathways can become vulnerable as well. The queen of *Blepharidatta canops* Kempf, 1967 (Formicidae: Myrmicinae) herself has a phragmotic head. When the nest is under attack, the workers stack eggs in the brood chamber; the queen then remains in the chamber to block its entrance and protect the young (Fig. 3A), her head specifically shaped to protect the brood chamber opening and no other entryway in the nest (Brandão et al. 2001). In the genus *Pheidole* Westwood, 1839 (Formicidae: Myrmicinae) the queen uses "reverse phragmosis" where a morphologically flattened posterior "plug-like modification of the gaster" defends the brood chamber in a manner otherwise similar to the tactic of *B. canops* (Brown, 1967).

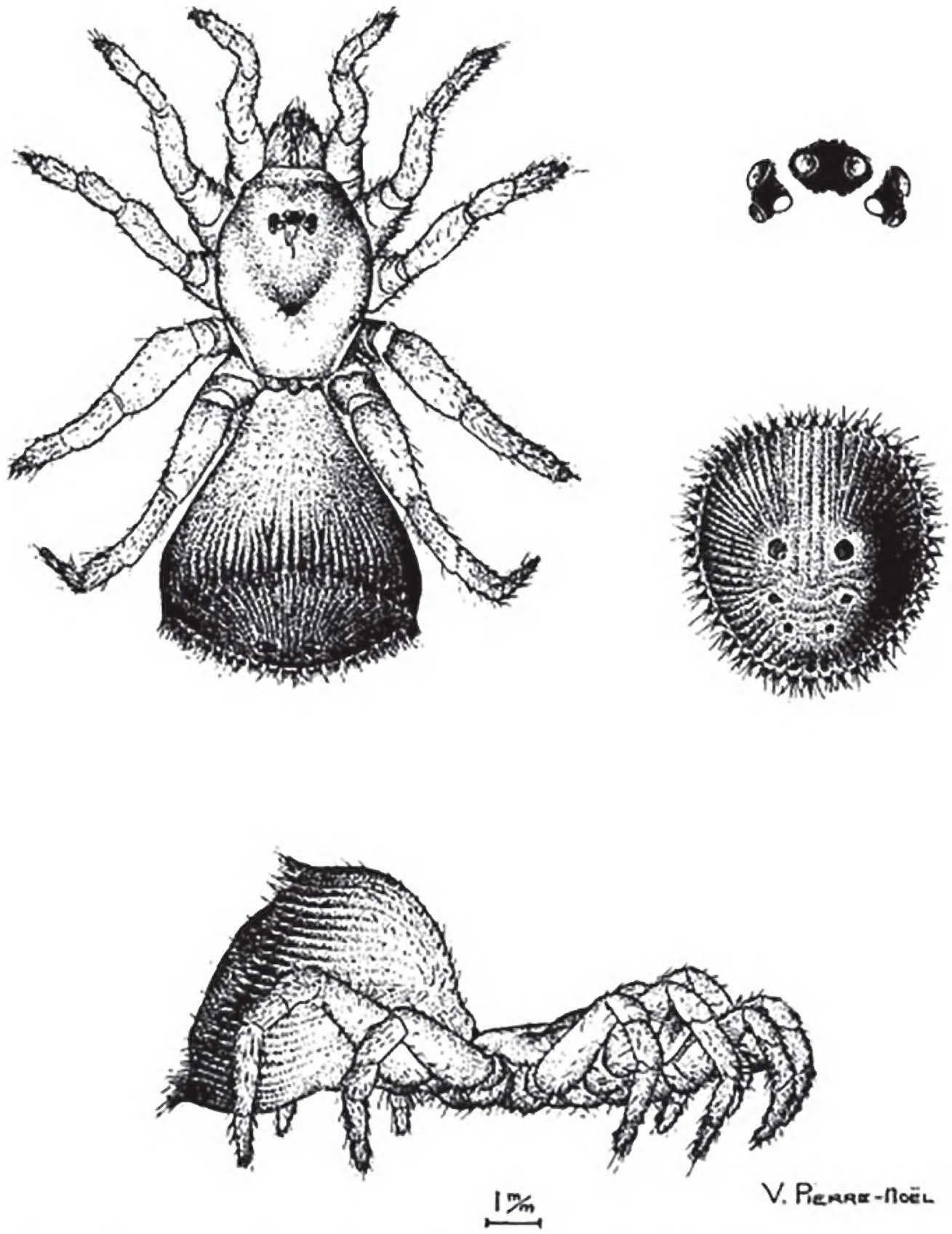

Figure 2. *Cyclocosmia truncata* (Hentz, 1841) (Halonoproctidae) (Gertsch and Wallace 1936).

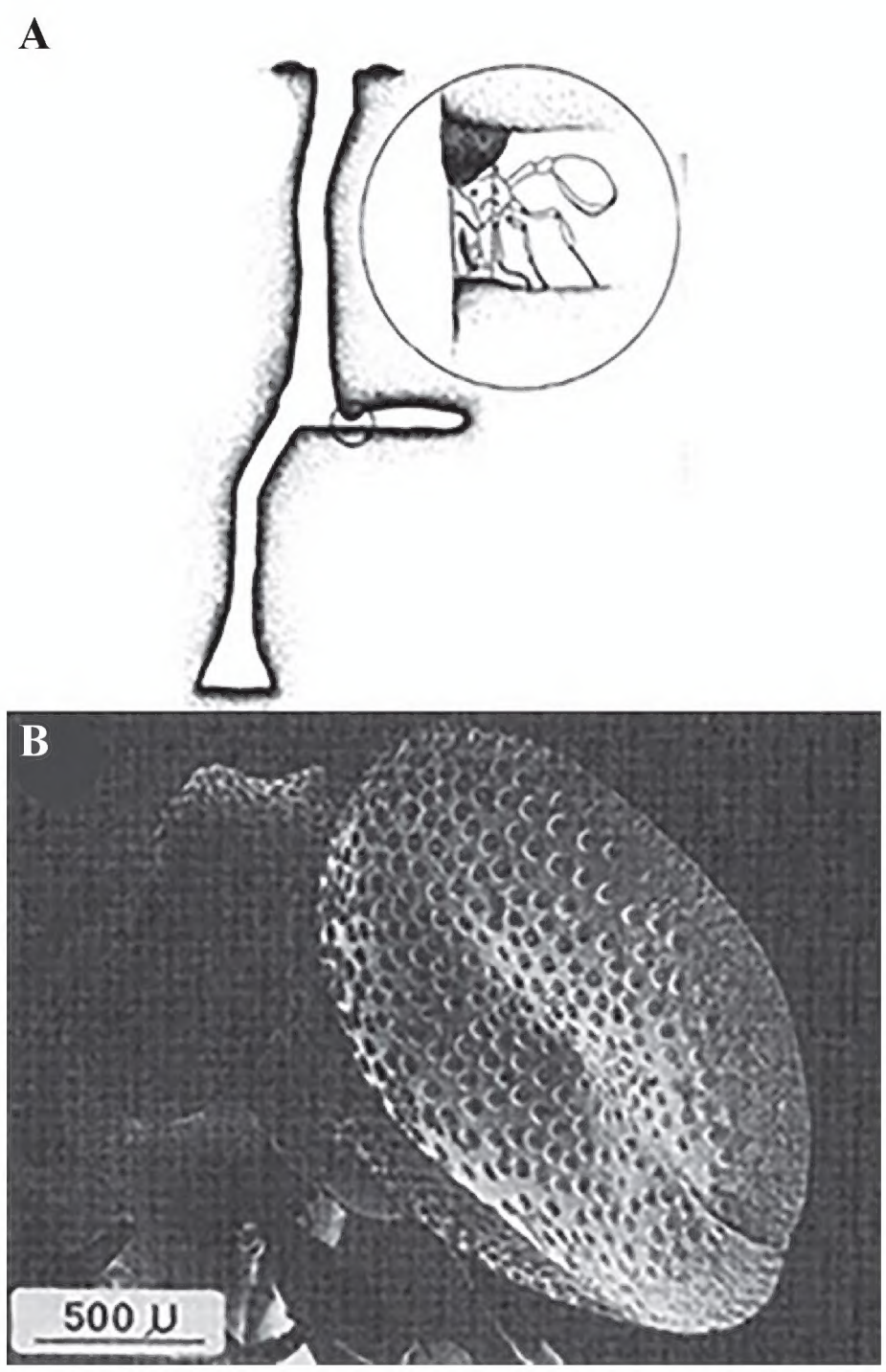

Figure 3. Phragmosis and camouflage examples. **A.** Diagram of nest and queen of *Blephairdatta canops* Kempf, 1967 (Formicidae: Myrmicinae) using head and pronotum to block brood chamber (Brandão et al. 2001); **B.** Phragmotic head surface of *Cephalotes varians* (Smith, 1876) (Formicidae: Myrmicinae) soldier (Wheeler & Holldobler, 1985, as *Zacryptocerus varians*).

Some ants also use camouflage in conjunction with phragmosis. The phragmotic head of some *Cephalotes* species commonly accumulates dirt in the shallowly concave disk (Wheeler 1942); soil particles are trapped in tiny hairs arising in numerous pores (Fig. 3B), thereby using both camouflage and phragmosis for defense (Wheeler and Holldobler 1985).

Some Coleoptera also defend themselves with phragmosis. Keyhole ambrosia beetles such as *Amasa truncata* (Erichson, 1842) (Curculionidae) have truncate elytra forming a flat circular posterior (Flechtmann and Cognato 2011). The female bores headfirst into *Eucalyptus* wood and creates multiple chambers for the eggs (Moore 1962; Robinson 1987). The truncate elytra block the burrow, protecting those chambers, their fungal food sources, and their brood (Bentz and Jönsson 2015). In the same family, the genus *Ips* DeGeer 1775 has several species with slightly truncate and concave elytra, sometimes with spikes on the edges of the disk or with many stiff hairs (Fig. 4; Eickwort et al. 2006).

In these examples from terrestrial animals, a flattened and hardened anterior or posterior surface has evolved as defense against predation. We hypothesized that a similar

Figure 4. *Ips pini* (Say, 1826), left lateral (Cognato 2015).

phenomenon may have occurred in another group of animals that defends a small opening, the larvae of case-bearing Trichoptera. Larvae of various tube-case-making caddisflies in subterorder Phryganides construct many particular shapes of cases using silk and a wide variety of building materials assembled in characteristic patterns. These cases have evolved for camouflage, physical protection, and as a respiratory aid (Williams et al. 1987; Wiggins 1996). Each of these cases has a vulnerable chokepoint at the anterior opening and sometimes at a posterior opening. We propose that these exposed openings have provided selective pressure to evolve phragmotic defense techniques in at least some species of Trichoptera.

Furthermore, our hypothesis is that phragmosis has evolved independently in a variety of Trichoptera genera along different evolutionary pathways either alone or possibly in conjunction with filter feeding or other adaptations. Examples of species that may exhibit phragmosis in Trichoptera include at least those in Table 1. Brachycentridae, Goeridae, and Limnephilidae are families with several examples of probable phragmosis in Trichoptera, usually involving a flat head. Examples in Goeridae appear to have phragmotic shields on the head, pronotum, and/or mesonotum, either alone or in combination (Nozaki and Shimura 2020). Although less common, some species may use posterior plates for defense of a posterior case opening, as suspected in genera *Setodes* (Leptoceridae) and *Limnephilus* (Limnephilidae).

We think the three necessary criteria for phragmosis are as follows: (1) there must be a small entryway to be defended, (2) the morphology of the phragmotic shield should correspond with the shape of that entryway, and (3) the phragmotic shield must be deployed in the entryway whenever an intruder attacks or threatens to attack. Although phragmosis was originally proposed as a strategy to defend a stationary opening to an underground nest (Wheeler 1927) and later expanded to accommodate burrows of frogs in soil or wood or of beetles in wood, we recommend revising the definition of this phenomenon further to include its use with portable cases having similarly defensible openings. We propose that case-making Trichoptera larvae with flat, disk-shaped heads or anal ends, such as those listed in Table 1, are examples of species with probable phragmotic defense, complying with at least the first two of these criteria.

Table 1. Selected Trichoptera species with morphological shields that may be phragmotic.

Family	Species	Case	Phragmotic surface (shield)	Habitat	Food/ feeding method	References illustrating shield
Apataniidae	*Allomyia scotti* Wiggins, 1973	Small stones	Head (with horns)	Lotic-erosional, hygropetric	Periphyton/scraper	Wiggins 1996
	Apatania theischingerorum Malicky, 1981	Small stones	Head	Lotic-erosional	Periphyton/scraper	Waringer and Graf 2011
Antipodoeciidae	*Antipodoecia turneri* Mosely, 1934	Small stones	Head + pronotum	Lotic-erosional	Unknown	St Clair et al. 2018
	Anomalopsyche minuta (Schmid, 1957)	Small stones	Head + pronotum	Lotic erosional	Periphyton/scraper	Pes et al. 2018
Beraeidae (Wallengren, 1891)	*Beraeamyia squamosa* Mosely, 1930	Small stones	Head	Lotic-erosional	Unknown	Waringer and Graf 2011
	Beraea fontana Wiggins, 1954, etc.	Small stones	Head + pronotum	Eucrenon muck (argyllal)	Fine Particulate Organic Matter (FPOM)/ gatherer	Wiggins 1996
	Beraeodes minutus (Linnaeus, 1761)	Small stones	Head	Variable	Periphyton/Scraper	Waringer and Graf 2011
Brachycentridae	*Brachycentrus americanus* Banks, 1899	Plant material	Head	Lotic-erosional	FPOM & prey/filterer, periphyton/scraper	Wiggins 1996
	Brachycentrus maculatus (Fourcroy, 1785)	Fine sand	Head	Lotic-erosional	FPOM, prey, periphyton/filterer, predator, scraper, gatherer	Rinne and Wiberg-Larsen 2017
	Dolichocentrus sakura Nozaki, 2017	Fine sand	Head	Lotic-erosional, -depositional	Unknown	Nozaki 2017
	Micrasema rickeri Ross & Unzicker, 1965	Plant material	Head	Lotic-erosional	Mosses/shredder	Chapin 1978
	Micrasema minimum McLachlan, 1876, etc.	Fine sand	Head	Lotic-erosional	Mosses, periphyton/shredder, scraper	Waringer and Graf 2011
	Tsudaea kitayamana (Tsuda, 1942)	Sand grains with moss attached	Head	Lotic-erosional	Mosses/shredder	Nozaki 2009
Goeridae	*Goera rupicola* Nozaki & Shimura, 2020	Small stones & larger ballast stones	Head + pronotum + mesonotum	Lotic-erosional rock surface (hygropetric)	Periphyton/scraper	Nozaki and Shimura 2020
	Goera calcarata Banks, 1899	Small stones & larger ballast stones	Head	Lotic-erosional rock surface	Periphyton/scraper	Flint 1960
	Goeracea genota Ross, 1941	Small stones & larger ballast stones	Pronotum + mesonotum	Lotic-erosional	Periphyton/scraper	Wiggins 1996
	Lepania cascada Ross, 1941	Small stones	Head + pronotum + mesonotum	Organic muck of springs	FPOM/gatherer	Wiggins 1996
	Silo pallipes (Fabricius, 1781), etc.	Small stones & larger ballast stones	Head + pronotum + mesonotum	Lotic-erosional	Periphyton/scraper	Waringer and Graf 2011; Rinne and Wiberg-Larsen 2017
	Lithax obscurus (Hagen, 1859), etc.	Small stones & larger ballast stones	Head + pronotum + mesonotum	Lotic-erosional	Periphyton/scraper	Waringer and Graf 2011
	Larcasia akagiae Nishimoto & Tanida, 1999	Small rock fragments	Head (with knobs)	Lotic-erosional	Periphyton/scraper	Nishimoto et al. 1999
Lepidostomatidae	*Lepidostoma emarginatum* (Ito, 1985)	Leaf panels	Head	Springbrooks	Coarse Particulate Organic Matter (CPOM)/shredder-detritivore	Ito 1985
	Theliopsyche melas Edwards, 1956	Fine sand	Head	Springbrooks	Unknown	Wiggins 1996
Leptoceridae	*Setodes incertus* (Walker, 1852), etc.	Coarse sand	Abdominal segment X	Burrowing in lotic sand	FPOM, prey/gatherer, predator	Merrill and Wiggins 1971
Limnephilidae	*Cryptochia pilosa* (Banks, 1907)	Wood	Head	Wet riparian wood, leaves	CPOM/shredder-detritivore	Wisseman and Anderson 1987
	Cryptothrix nebulicola McLachlan, 1867	Sand	Head	Lotic-erosional	Prey/filtering predator	Waringer and Graf 2011
	Drusus chrysotus (Rambur, 1842)	Sand	Head	Lotic-erosional	Prey/filtering predator	Waringer and Graf 2011
	Ecclisopteryx madida (McLachlan, 1867)	Sand	Head + pronotum	Lotic-erosional	Periphyton/scraper	Waringer and Graf 2011
	Limnephilus extricatus McLachlan, 1865	Sand	Abdominal segment X	lentic	CPOM, prey, periphyton/ shredder, predator, scraper	Waringer and Graf 2011
Rossianidae	*Rossiana montana* Denning, 1953	Coarse sand	Head + pronotum	Springbrooks, hygropetric	Woody debris, fungi/gouger, shredder	Wiggins 1996
Sericostomatidae	*Fattigia pele* (Ross, 1938)	Fine sand	Head	Burrowing in sand of springbrooks	FPOM/gatherer	Wiggins 1996; this study
	Notidobia ciliaris (Linnaeus, 1761)	Fine sand	Head	Burrowing in sand, springbrooks to streams	CPOM/shredder	Rinne and Wiberg-Larsen 2017

To test this phragmosis hypothesis, we needed to observe the third criterion, the actual use of an apparent shield by a case-making caddisfly larva to block its opening when disturbed by a predator.

Cathaptosis

In our pursuit of examples of caddisfly phragmosis we suspected another type of defense designed to protect the

opening of a portable and otherwise protective dwelling. We define "cathaptosis" as any method by which an animal defends itself at a vulnerable opening of such a portable case or shell by holding the substrate tightly against the opening. This behavior has been previously described for case-bearing larvae of camptosomate leaf beetles such as *Neochlamisus gibbosus* (Fabricius, 1777; as *Arthrochlamys plicata* Fabricius, 1798) and *Exema canadensis* Pierce, 1940 (both Chrysomelidae: Crytocephalinae) (Wallace 1970; Agrain et al. 2015) which construct elliptical or cylindrical, portable and protective cases from bits of their frass, but the described behavior was not named. The case's single opening can be transverse or oblique. When the larval beetle and its case are in the cathaptotic position, the case often is camouflaging, appearing to be a piece of caterpillar frass (Chaboo 2011). The larva has stout, curved tarsal claws for better grip on the substrate when it defensively retracts its legs into its fecal case (Root and Messina 1983).

Unlike phragmosis, this defense does not require a specialized flattened morphological adaptation, although some beetle species do have flattened heads to press against the substrate. An example of cathaptosis in animals other than insects is freshwater pulmonate snails (Pulmonata). These gastropods use their slime and foot as a suction disk to grip the substrate. When attacked, the snail draws itself into its shell, causing difficulty for a predator to lift the shell from its substrate to access the soft-bodied snail (personal observation).

In both beetles and snails, the animals have developed a method with which to gain a purchase on their substrate sufficient to defend themselves within their protective, portable cases. We think the three necessary criteria for cathaptosis are as follows: (1) there must be a protective, portable case or shell with an entryway to be defended; (2) the morphology of the case and its opening should correspond with the shape of the substrate surface on which the animal lives; and (3) when an intruder attacks or is threatening, the entryway must be sealed by the animal holding the entryway tightly against the substrate.

Unlike case-bearing leaf beetles, for which the case opening is often transverse with the length of the case, case-bearing caddisflies living in lotic waterways must carry their cases horizontal with the flow of the water in a manner that provides least resistance to the water. Therefore, to meet the second criterion, the opening of a case of a stream-dwelling caddisfly larva with cathaptotic behavior will be usually oblique (or beveled) or ventral to apply against the substrate most effectively. We propose that case-making Trichoptera larvae living in streams on exposed substrates and with beveled or ventral anterior case openings, such as those listed in Table 2, may be examples of species that perform cathaptotic defense and that caddisflies with cases meeting the first two criteria can be tested for cathaptotic behavior by observing the third criterion.

To test this cathaptosis hypothesis, we needed to observe the third criterion, the actual fastening of a case to substrate by a case-making caddisfly larva to block its opening when disturbed by a predator.

Methods

To test our hypothesis for phragmosis, we observed the predator-prey interaction of case-making larvae of two Trichoptera species found locally in the Southern Appalachian Mountains when confronted with predators common in their habitats. The larva of *Goera calcarata* Banks, 1899 (Goeridae) makes a tubular case with lateral ballast stones for stability in fast-flowing water as it scrapes periphyton from the top surfaces of rocks in lotic-erosional habitats (Wiggins 1996). The larva of *Fattigia pele* (Ross, 1938) (Sericostomatidae) makes a case of fine sand and burrows in the sand of mountain springbrooks to gather fine organic particles (Wiggins 1996).

Mature larvae of *G. calcarata* were collected from the tops of stones in a first-order stream at 34°45.366'N, 82°51.372'W, ca. 300 m a.s.l., and young larvae of *F. pele* were sifted from sand in a springbrook at 35°22.2'N, 83°6.6'W, ca. 1,520 m a.s.l. Available predators at those sites included larvae of *Acroneuria abnormis* (Newman, 1838) (Plecoptera: Perlidae) and *Corydalus cornutus* (Linnaeus, 1758) (Megaloptera: Corydalidae). Specimens of both the Trichoptera and the predators were transported back to the

Table 2. Selected Trichoptera species with cases that may be used in cathaptosis.

Family	Species	Case	Anterior case opening	Habitat	Food/ feeding method	References illustrating case
Apataniidae	*Apatania arizona* Wiggins, 1973	Rock fragments	Oblique (final instar)	Springbrooks, lakes	Periphyton/scraper	Wiggins 1996
Calamoceratidae	*Anisocentropus pyraloides* (Walker, 1852)	Two dead leaves	Ventral	Lotic-depositional, in debris, on rocks (final instar)	Coarse Particulate Organic Matter (CPOM)/shredding detritivore	Wiggins 1996
	Heteroplectron californicum McLachlan, 1871	Excavated stick	Oblique	Lotic- depositional, in debris & on wood	CPOM/shredding detritivore	Wiggins 1996
Glossosomatidae	*Glossosoma intermedium* (Klapálek, 1892)	Rock fragments	Ventral	Lotic-erosional, on rocks	Periphyton/scraper	Ross 1944
Helicopsychidae	*Helicopsyche borealis* (Hagen, 1861)	Sand grains	Ventral	Lotic, lentic	Periphyton/scraper	Wiggins 1996
Leptoceridae	*Ceraclea ancylus* (Vorhies, 1909)	Fine sand	Oblique	Lotic depositional, on rocks	Periphyton/scraper	Resh 1976
Molannidae	*Molanna flavicornis* Banks, 1914	Rock fragments	Ventral	Lotic-depositional, lentic	Periphyton, Fine Particulate Organic Matter (FPOM), prey/ scrapers, gatherers, predators	Wiggins 1996

laboratory with stream water in separate plastic bags on ice and were kept alive and starved in refrigerated stream water until their interactions could be documented a few days later.

The observation arena was a wide glass dish filled with stream water. A caddisfly and a predator were introduced into the arena and observed for a few minutes as they warmed to room temperature. We observed and recorded the interactions through a Celestron Microscope Pro® Model #44308 attached to a computer.

To test our hypothesis of cathaptosis, we observed the case and behavior of a Chinese species of *Ascalaphomerus* Walker, 1852 (Calamoceratidae). Larvae of an *Ascalaphomerus* species were captured on pieces of wood in a pool of a mountain creek (P.R. China: Zhejiang Province, Li-shui City, Yun-he County, Dian-qing-shan Village, Yuntan-xi Stream 28°9.72'N, 119°41.532'E, ca. 320 m, 9 August 2022) and brought with the wood to the laboratory for testing. Leaf litter, stones, and woody debris (twigs) were placed with the larvae in a rearing chamber. Instead of using a living predator, we gently agitated a test animal with a probe. The response of the larva was recorded with an Olympus TG-6 digital camera (Olympus, Beijing, China).

Results

For the experiment to test for phragmosis when disturbed by a stonefly or hellgrammite predator, each of the larvae of *F. pele* and *G. calcarata* quickly withdrew into its case to expose only the flattened front of the head (*F. pele*) or flattened top of the head and anterior nota (*G. calcarata*), behavioral responses consistent with phragmosis. This activity was recorded (Bishoff 2023a, 2023b, 2023c). The response was seen even when predators were absent; a small movement of the dish or even a shadow prompted the animal to retreat quickly into its defensive posture, presumably because these phenomena are clues to the presence of a predator.

For the experiment to test for cathaptosis, an *Ascalaphomerus* specimen responded to the probing activity by gripping the piece of wood tightly and pressing the case opening onto the wood. The larva also spun silk to anchor the lower edge of the case even more securely to the wood. This activity and the silk anchor were recorded (Peng et al. 2023).

Discussion

Recent studies have demonstrated that flat-headed structure in some *Drusus* species (Limnephilidae) is adapted to the creation of vortices for entrapping prey (Waringer et al. 2015, 2021) and is also associated with the use of filtering bristles for predation (Pauls et al. 2008; Vitecek et al. 2020) The musculature of these flattened larval heads is very similar to that of larvae of other *Drusus* species with normal, convex heads and lacking filtering bristles (Zittra et al. 2022). *Drusus muelleri* McLachlan 1868 is a species that has long spines on the lateral edges of the head (Graf et al. 2005) that apparently help dissipate the force of the water, relieving hydraulic stress. These sharp points could also help to deter predators that might attempt to remove them from their cases, as may also be the defensive purpose of marginal elytral spines in some ambrosia beetles. We propose that this flat-headed morphology that has been associated with filtering predation or hydraulic adaptation may also be a structural component of phragmotic defense. It seems likely that larvae of *D. muelleri* and related species are using their flat heads not only to capture prey or maintain position in fast-flowing water, but also to protect themselves from predators, or a combination of these functions. It is unclear whether one function is a pre-adaptation of the other and, if so, the evolutionary direction of any pre-adaptation.

However, larvae with flat heads also live in a wide variety of other habitats and feed with various other methods on a wide range of food resources. For example, caddisflies with flat, apparently phragmotic structure inhabit not only fast-flowing water, but also organic muck, drifting sand, hygropetric habitats, or quiet pools with accumulations of organic debris (Table 1). Furthermore, they feed in ways other than predation, including shredding large pieces of detritus, scraping periphyton from hard and stable substrates, and gathering or filtering small detritus particles (Table 1).

Interestingly, there are also examples of flattened heads in some retreat makers of the suborder Annulipalpia. The larvae of at least some species of *Macrostemum* (Hydropsychidae) have flat heads that a larva may use to block the anterior opening of the side channel of its highly specialized retreat or to help direct the flow of water through its filternet, or both.

For the experiment to test for cathaptosis, the "case" of the *Ascalaphomerus* species is actually a small stick. Instead of assembling a case with silk and pieces of substrate, a larva of this genus gouges the pith from the axis of a single stick (or occasionally some other piece of wood), then transports the hollowed stick or piece of wood as though it were a case constructed of smaller pieces of substrate. The anterior opening of the case is beveled so that if it is in a cathaptotic position, it will be held at an angle to the substrate. During daytime, the substrate is usually a larger, dead tree limb lying on a stream bottom in slowly moving marginal water. When the *Ascalaphomerus* larva is gripping the dead limb in cathaptosis, its "case" appears to be a broken twig of the tree limb. Larvae of this genus typically remain still and cathaptotic during daylight hours, protected by camouflage from visual hunters. At night they moved more freely, shredding dead plant debris or capturing small animals for food.

In Trichoptera, potential examples of phragmosis (Table 1) seem to be more common than of cathaptosis (Table 2).

Conclusions

For an animal that lives in a burrow, nest, or portable case or shell, the threshold between their home and the outside

world is a transition portal of vital importance. It is the animal's point of departure from a relatively safe haven to access other vital resources. This vulnerability has served as selective pressure, resulting in the evolution of the defense techniques of phragmosis and cathaptosis. Both techniques seal the opening, but in very different ways.

We have demonstrated the behavioral components of these defensive behaviors for three species and provided lists of some species whose larvae and cases meet their respective, necessary structural criteria. We encourage colleagues to test these hypotheses with the species listed in Tables 1 and 2 and with any other species appearing to meet the structural requirements of these defensive strategies to determine whether the associated behavioral components also occur.

Author Contributions

Conceptualization: MJB, JCM. Literature review: MJB. Investigation: MJB, LP, H-mZ. Original draft: MJB. Review/editing: MJB, LP, H-mZ, JCM. Supervision: JCM.

Conflicts of Interest

The authors declare no conflicts of interest. No other employees of our universities had a role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

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